5

The Relation of Oxygen Consumption to Temperature in Some Tropical, Temperate and Boreal Anuran Amphibians[1]

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(Text-figures 1 & 2)

PREVIOUS studies on the geographic variation in climatic adaptation for poikilotherms have revealed much of physiological, ecological and evolutionary importance. The literature in this field has been thoroughly reviewed by Prosser (1955) and Bullock (1955). In respect to amphibians, investigations on the geographic variation of developmental adaptation in anurans (e.g. Moore, 1949; Volpe, 1954) have been particularly significant. Relatively little data, however, are available in which metabolic rate and temperature have been compared in amphibians from different latitudes. It is the purpose of this study, therefore, to present an analysis of the respiratory metabolism of some tropical, temperate and boreal anurans when compared at two similar temperature levels.

The tests were carried out on five species of tropical frogs: *Hyla maxima* and *Hyla crepitans* (Hylidae); *Leptodactylus typhonius* and *Eupemphix pustulosus* (Leptodactylidae) and *Prostherapis trinitatis* (Dentrobatidae). The temperate and boreal forms included the toads *Bufo boreas boreas* and *Bufo boreas halophilus* (Bufonidae); and the frogs *Rana clamitans* and *Rana sylvatica* (Ranidae) and *Hyla crucifer*.

The experimental work was undertaken at Simla, field station of the Department of Tropical Research, New York Zoological Society, Arima Valley, Trinidad, B.W.I., and the Department of Zoology, Columbia University, New York, from December, 1954, to July, 1955.

We wish to thank Ernest Karlstrom of the University of California for sending us the *Bufo boreas* material from California. The assistance of Rosemary Kenedy during the work at Simla is also gratefully acknowledged. The respirometers were kindly loaned to us by F. John Vernberg of Duke University.

Materials and Methods

All tropical frogs were collected in the immediate vicinity of Simla in the northern range of Trinidad at an elevation of around 800 ft. between December 26 and March 30. *Hyla crucifer* was collected near New York City in late April and early May, and *Rana clamitans* and *Rana sylvatica* from Bondville, Vermont (1,500 ft.), on July 3 and 4. Breeding individuals of *Bufo boreas boreas* were taken seven miles northwest of Juneau, Alaska (sea level), between June 1 and 10, and post-breeding forms of *Bufo boreas halophilus* from California at the following localities: Richmond, Contra Costra Co. (sea level); Russian River area, Sonora Co. (sea level to 1,000 ft.) and Sequoia National Park, Tulare Co. (7,500 ft.) between June 1 and 19. The five tropical species ranged in weight from 0.5 to 45.5 gms., and the four temperate and boreal species from 0.84 to 56.1 gms.

After collecting, the tropical frogs were maintained in aquaria at room temperature (20-25° C.), and the temperate and boreal forms were kept in aquaria in a constant temperature (15° C.) room. All were fed regularly on adult or larval insects.

Closed system volumetric respirometers of the type developed by Flemister & Flemister (1951) were employed for the determination of the respiration rates. Tests were conducted in water baths maintained at 25 ± .5° C. and 10 ± .5° C.

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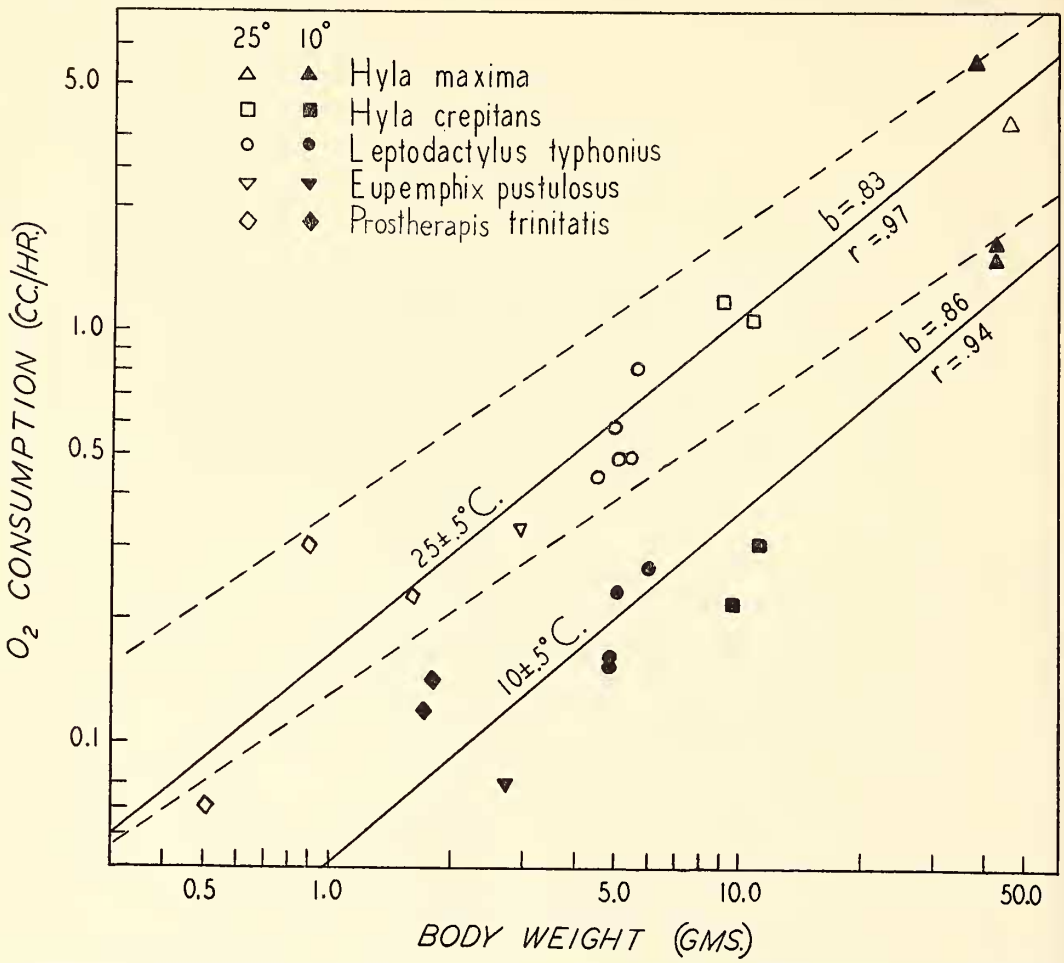
[3]This study was aided in part by the Arctic Institute of North America through funds granted by the Office of Naval Research.



TEXT-FIG. 1. The relation of oxygen consumption to weight in five species of tropical anurans at two temperature levels (b = regression coefficient; r = coefficient of correlation). Dashed lines represent regression slopes for temperate species.

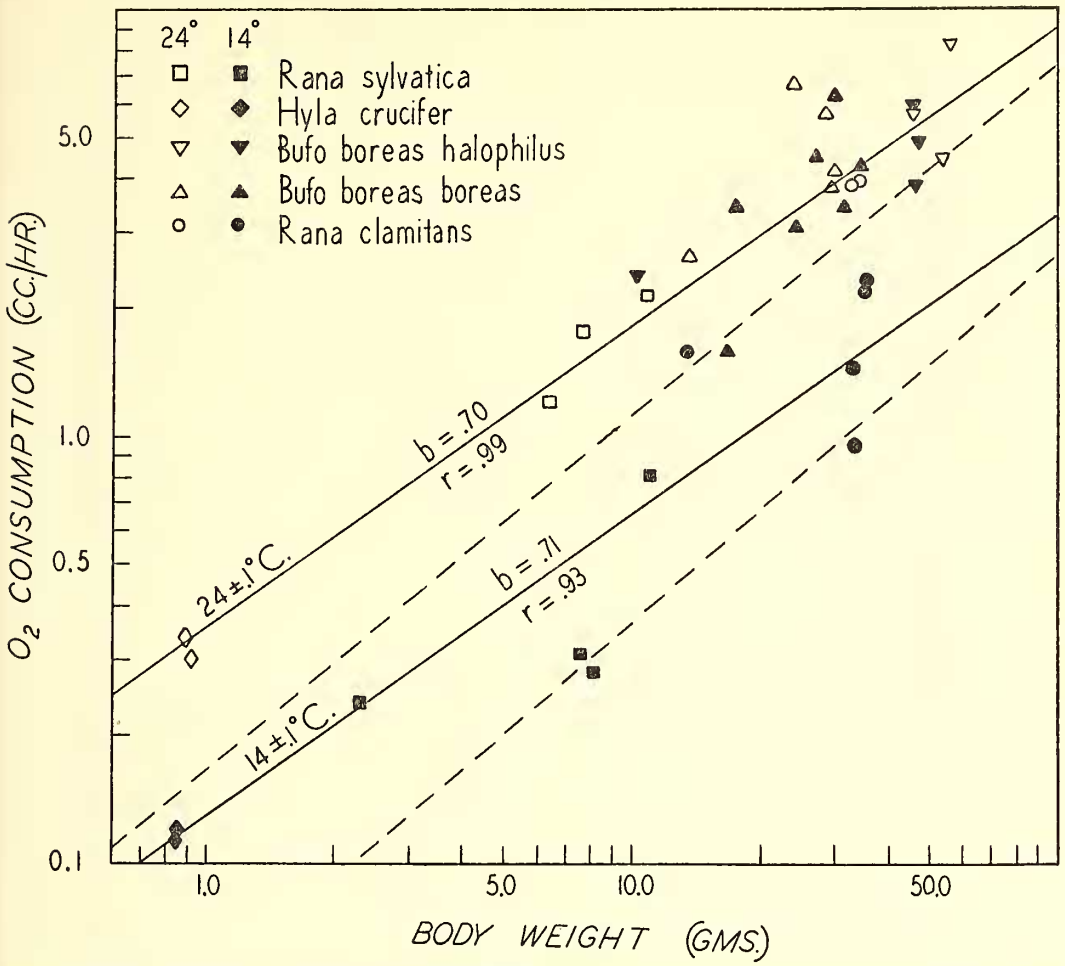
for the tropical forms and 24 ± .1° C. and 14 ± .1° C. for the temperate and boreal animals. After allowing a half hour for thermal equilibrium the tests were then run for a period of three or four hours. The volumes obtained for oxygen consumption have been corrected to standard temperature.

RESULTS

Text-figures 1 and 2 represent the double-logarithmic regression plots of weights to metabolism where the log of the rate of oxygen consumption (cc./hr.) equals log a + b log W, or metabolic rate equals aW^b, the constants a and b being the regression coefficients of the intercept and slope and W the wet body weights (gms.). Because of the slight depression for the values at 14° C. the data for *Bufo boreas*, although plotted, were not included in computing the regression lines for Text-figure 2.

At both temperature levels the respiratory rates for the tropical frogs averaged lower than those from the northern latitudes at similar temperatures. This appears to be especially evident when we compare the smaller animals, and is reflected in a steepening of the slope for the tropical weight regression coefficients. Although the average regression coefficient of .71 for the temperate animals at the two testing temperatures is but slightly higher than an exponent of ⅔ (.67) that we might expect in keeping with the surface law of metabolism (metabolism/time = $aW^{2/3}$), the average slope of .84 for the tropical species seems significantly greater. There appears to be little correlation between temperature and regression slope in animals from the same general latitude.

With the exception of *Bufo boreas*, the temperature coefficients (Q_{10}) did not vary significantly between the tropical and temperate



TEXT-FIG. 2. The relation of oxygen consumption to weight in four species of temperate and boreal anurans at two temperature levels (b = regression coefficient; r = coefficient of correlation). Dashed lines represent regression slopes for tropical species. Data for *B. boreas* were not used in plotting the regression lines.

species (Table 1). The oxygen consumption rates for *Bufo boreas* at both temperature levels showed little variation both within and between the Alaskan and Californian forms. In fact, at both 14° and 24° C. the two races of *Bufo boreas* showed a metabolic rate typical of the temperate frogs tested at 24° C. This relative insensitivity to temperature change is reflected in their low temperature coefficients.

Discussion

The weight regression coefficients (.703 and .707) for the temperate animals studied here are supported by the findings of others. Davison (1955) found a value of approximately ⅔ (.67) for the exponent in seven species of temperate anurans (weight range 1 to 350 gms.) that he measured at 25° C., and Rubner (1924) reports an exponent of .67 for *Rana esculenta*. Regression coefficients of .80 and .85 are given by Scholander *et al.* (1953) in the tropical and arctic animals (fishes, crustaceans, insects and spiders) that they measured at 0° C. (arctic species) and 20-30° C. (tropical species). No shift in the weight regression slope is apparent between the arctic and tropical forms. Because of the limited number of species tested by us in the present study, the steeper regression slopes (.825 and .861) found in the tropical species can not be considered as conclusive.

The compensatory metabolic rates exhibited by the northern or cold-adapted anurans studied here are in keeping with the general concept (Bullock, 1955) that activity rates are greater at a given temperature in cold-blooded animals from northern latitudes when compared with the same or closely related southern forms. Scholander *et al.* (1953) state that climatic adaptation in terrestrial poikilotherms is not

TABLE 1. SUMMARY OF DATA ON RESPIRATORY METABOLISM FOR ADULT TROPICAL, TEMPERATE AND BOREAL ANURANS AT TWO TEMPERATURE LEVELS.

Tropical Species	Sample Size	Weight (gms.)		QO_2 (cc./gm./hr.)		Weight (gms.)		QO_2 (cc./gm./hr.)		Q_{10}
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	
		10 ± 0.5° C.				25 ± 0.5° C.				
Hyla maxima	4	41.9-42.1	42.0	.035-.039	.037	37.4-45.5	41.4	.070-.121	.095	1.88
Hyla crepitans	4	9.6-11.1	10.3	.022-.026	.024	9.1-10.7	9.9	.101-.132	.116	2.87
Leptodactylus typhonius	9	4.8-6.0	5.1	.032-.046	.038	4.5-5.6	5.1	.098-.147	.115	2.10
Eupemphix pustulosus	2		2.7		.028		2.9		.117	2.61
Prostherapis trinitatis	5		1.7	.039-.071	.055	0.5-1.6	1.0	.139-.324	.201	2.38
Temperate and boreal species		14 ± 0.1° C.				24 ± 0.1° C.				
Rana clamitans	6	33.1-35.4	34.2	.028-.073	.051	33.0-34.4	33.2		.117	2.29
Rana sylvatica	6	7.5-11.0	8.8	.059-.075	.067	6.4-10.7	8.2	.186-.233	.206	3.07
Hyla crucifer	4		0.85	.097-.148	.122	0.89-0.91	0.9	.333-.382	.357	2.93
Bufo boreas halophilus	6	46.0-47.1	46.4	.084-.141	.107	45.6-56.1	51.7	.083-.147	.119	1.11
Bufo boreas boreas	9	24.2-34.8	29.5	.111-.210	.152	24.8-30.0	28.1	.131-.268	.181	1.19

significantly reflected by over-all oxygen consumption in the tropical and arctic insects and spiders that they tested at 0° and 20° C. Prosser (1955) also concludes that metabolic differences in populations are to be found in aquatic but not in terrestrial poikilotherms. If we consider the amphibians studied here as semi-terrestrial, we should then expect to find a significant, but not pronounced, difference in climatic adaptation between the tropical and northern forms. This appears to be the case. It would seem that a similar study of tropical and temperate reptiles would be of particular interest in this respect.

It is also generally accepted (Bullock, 1955) that cold-adapted poikilotherms tend to show a lower Q_{10} when compared with the same or closely related warm-adapted species. This concept becomes apparent among the anurans of this study only in the toad *Bufo boreas.* The other frogs show no significant variation in Q_{10} between tropical and temperate forms (Table 1). This seemingly inherent low Q_{10} for *Bufo boreas* could have been a contributing factor in its successful northern extension into southern Alaska. It is interesting to note, however, that in *Rana sylvatica,* which ranges even further north than *Bufo boreas,* we find no inherently lower temperature coefficient. These results can probably be partially explained by the limited number of determinations made as well as by the fact that we are here grossly comparing different species. Moreover, familial differences such as the more terrestrial habits of *Bufo boreas* could conceivably explain the dissimilarities. Breeding condition, size and seasonal fluctuations may also have had an influence. However, with the exception of *Hyla crucifer,* all northern animals were collected between June 1 and July 4, and only adults of similar weight within a species were used in the determination of the temperature coefficients. *Bufo boreas boreas* was the only form in breeding condition at the time of collecting. It is surprising that individuals of *Bufo boreas* exhibited such a persistently similar metabolic picture, coming as they did from two places so widely separated in latitude and altitude (sea level to 7,500 ft.).

There is good evidence in support of the conclusion (for references see Dehnel, 1955) that at their normal environmental temperatures, activity rates of closely related northern and southern animals are usually similar. The annual range of mean monthly temperatures for Juneau vary from −1.6° C to 13.0° C (1921-1950) with an annual mean of about 5.8° C. compared with a range of 25.6° to 27.3° C. and an annual mean of 26.5° C. for Trinidad (Port-of-Spain). If we take the mean monthly temperature for June at Juneau (12.0° C.) and the average January to March monthly temperature for Simla (ca. 24° C.), we can then use the lower testing temperature (14° C.) for *Bufo boreas boreas* and the upper testing temperature (25° C.) for the tropical species as being reasonably close to their normal mean habitat temperature at the time of collecting. In examining the two extreme latitudinal forms of similar size (Table 1), we find *Bufo boreas boreas* with a mean oxygen coefficient (QO_2) of .152 at 14° C., which is higher than that of all but one of the tropical frogs tested at 25° C. At their normal habitat temperatures, then, the northern species showed the more active metabolism. Other studies (Scholander *et al.,* 1953, and Tashian, 1956) showed a higher QO_2 for the tropical forms at their normal environmental temperatures.

Summary

1. The oxygen consumption of five species of tropical frogs from Trinidad, B.W.I., was determined and compared with that of four species of temperate and boreal anurans from Vermont, New York, California and Alaska at two temperature levels.

2. The respiratory metabolism for the northern forms averaged higher than that of the tropical animals at both temperatures. This higher metabolism for the cold-adapted animals is more evident in the smaller species, and is reflected in a steepening of the weight regression slope for the tropical species at both temperature levels.

3. With the exception of a lower Q_{10} for both races of *Bufo boreas* when compared with any of the other forms tested, no significant variation could be detected in the Q_{10} of northern and southern forms.

4. At their normal habitat temperatures, the northern species had a higher rate of respiration than the tropical species.

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